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Attenuation of Schedule-Induced Polydipsia with Textural but not Temporal Food Manipulations: Implications for the Oral Substitution Hypothesis

By

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DEDICATION

This thesis is dedicated to both my husband, Allen Burger, and my parents, Robert & Janet Allen, whose love and support gave me the opportunity to pursue a career, and the courage to achieve my goals.

Abstract

Schedule-induced polydipsia (SIP) is a phenomenon in which food deprived rats exhibit excessive drinking when placed on an FT 60-s schedule. Previous work has reported an inverse relationship between drinking levels and oral activity associated with feeding (Beck, Huh, Mumby & Fundytus, 1989). This relationship forms the basic premise of the oral substitution hypothesis - a theory which explains why drinking is the sensitized response in SIP. This hypothesis was tested by two experiments, each involving separate food manipulations designed to increase feeding behavior. In the first study, two food preparations, pit and shell, were administered to polydipsic rats. These food types differed in both form and texture but served to increase feeding behavior to a similar degree. The results lend support to the oral substitution hypothesis since drinking was reduced to normal levels in both conditions. In an attempt to explore the effects of temporal food manipulation, the second experiment delivered food granules of a size previously determined to induce polydipsia (Mumby & Beck, 1988) in four meals of 0, 14, 21 and 28 s duration. Although feeding behavior was progressively increased, drinking was not reduced from polydipsic asymptote except for powder controls. These data suggest that meal duration is not an important factor in SIP. The oral substitution hypothesis therefore proposes a relationship between drinking levels and the frequency of eating behavior with food texture an important feature in SIP.

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I. Introduction

Three decades ago, Falk (1961, cited in Roper, 1983) described a schedule-induced behavior whereby rats fed pellets intermittently developed excessive drinking. The properties of schedule-induced polydipsia (SIP) have since been investigated as well as the many factors that influence it. In addition, the research has led to a variety of theories attempting to explain SIP and why it develops.

Regarding the type of schedule, SIP occurrence is dependent on both the interfood interval and reinforcement magnitude. Essentially, a bitonic function exists such that intervals above and below the 60-180 s range produce less than optimal levels of water consumption (Falk, 1967; Flory, 1971). However, increasing the magnitude of the food reward has been shown to sustain SIP at interfood intervals as long as 12 min (Rosellini & Burdette, 1980). Research varying spout aperture has also shown that it is the amount of water consumed within the interfood interval that is important, not how long the rat drinks (Freed & Mendelson, 1977). In addition, the type of food delivered in these intermittent schedules has a great influence on the appearance of SIP. Pellets have traditionally been used and show a robust effect. Recent work has since shown that coarse granules produce SIP whereas powdered food does not (Mumby & Beck, 1988; Beck, Huh, Mumby & Fundytus, 1989). Similarly, liquid diets fail to produce SIP unless they are loaded with salt (Poling, Krafft, Chapman & Lyon, 1980). Finally, food and water deprivation levels influence the development of polydipsia. Falk (1971) reported that the amount of food deprivation relates inversely to the level of water consumption. The data suggest that optimal SIP is produced with rats at 80% of their preexperimental free-feeding weight. Asymptotic drinking levels are also increased by water deprivation (Brush & Schaeffer, 1974, cited in Roper, 1983). In contrast, infusing water into the stomach during food delivery fails to suppress additional drinking (Kenny, Wright & Reynolds, 1976).

The drinking response to the intermittent food schedule has distinct properties in and of itself. The robustness of SIP is demonstrated not only by its excessive nature, but also in the finding that rats will bar press for water following periodic food delivery (Roper, 1983). Other features include the fact that rats will also drink ethanol or salt solutions instead of water (Tang & Falk, 1986) - a finding that lends more credence to the strength of this response. It should be noted that polydipsia does not alter the topography of drinking since licking follows a normal rate (Roper, 1983). In addition, drinking tends to occur directly after eating in the interpellet interval, although this depends on the parameters of food delivery (Staddon, 1977). Finally, polydipsia, a difficult response to suppress once acquired, takes several sessions to fully develop (Wetherington & Riley, 1986). It is this particular feature of the drinking response that has largely been ignored or unaccounted for in many theories of SIP.

Explanations of SIP that encompass all of the properties associated with feeding and drinking are difficult to find. Those that can account for most of the findings, like motivational theories, are still not without flaws. Frustration, for example, is a subjective state that is difficult to measure (Roper, 1983). The fact that drinking and not some other behavior occurs to reduce the frustration or negative arousal caused by intermittent food delivery is also difficult to explain. SIP as a form of normal prandial drinking has failed to find full acceptance partly because it ignores the fact that excessive drinking is slow to develop, even in rats with a well developed prandial drinking repertoire (Staddon, 1977). Dry mouth theories, although supported by the finding of no SIP with unsalted liquid diets (Poling et al., 1980), are inadequate since SIP does not occur with dry powdered food (Beck et al., 1989; Mumby & Beck, 1988). According to Roper (1983), the complexity of SIP requires a new explanation that states not only why food elicits drinking but also why drinking is the facilitated response.

The sensitization theory of SIP proposed by Wetherington & Riley (1986) has provided adequate explanations for many features of polydipsia including its slow development, persistence, excessiveness and absence in no-food intervals. In essence, this theory proposes that repeated presentation of a stimulus, food, gradually leads to an increase in the elicited response, drinking. This repeated stimulation sensitizes the subject over time such that exaggerated responding persists and is easily elicted. If no food is presented, drinking does not occur since the eliciting stimulus has been removed. This theory therefore describes why food elicits drinking but does not state why drinking is the resultant response. The answer to this question lies in the finding that the level of drinking is inversely related to oral activity during feeding (Beck et al., 1989). In fact, this relationship forms the basic premise of the oral substitution hypothesis which suggests that SIP occurs as an oral response to the short uptake or feeding behavior associated with coarse textured food. Powder food, on the other hand, induces more feeding behavior and, because an oral substitute is not required, results in normal water intake.

The notion of drinking as an oral substitute for restricted eating comes from a response deprivation analysis of reinforcement (Timberlake & Allison, 1974). These authors refined Premack's principle, which stated that more probable behaviors reinforce less probable behaviors (Premack, 1962, 1963), to suggest that a more-restricted behavior will reinforce a less-restricted behavior. When food is restricted, so is its associated behavior - eating. Eating can therefore be described as a reinforcer for any other behavior if it is prevented from occurring at a level normally required. When eating behavior is no longer restricted compared to baseline or normal levels of consumption, then it will cease to act as a reinforcer. In addition, according to Timberlake (cited in Mazur, 1990), different reinforcers evoke specific behavioral systems. Food can therefore be said to elicit eating and other oral activities, including drinking, as required to meet baseline consummatory levels. In other words, drinking may act as an oral substitute for eating if the food type does not involve enough oral activity to satisfy the normal amount of eating, within the same period of time.

According to these theories, SIP is a sensitized response to repeated food presentation in the animal that is food deprived. If the eating response is sufficiently restricted by coarse textured food then, according to a behavioral systems approach, drinking will act as an oral substitute and will thereby become the sensitized response. With food that does not restrict eating (i.e. powder), drinking is not required as an oral substitute and therefore does not become sensitized with repeated food presentation. The concept of drinking as an oral substitute for eating follows logically if the anatomy of the striatum is also considered. The rostrolateral striatum has been shown to be involved in orofacial movements (Pisa, 1988a, 1988b). Based on this somatotopic organization, the initiation of both eating and drinking stems largely from the same area of the basal ganglia. If repeated presentation of food results in sensitization of a behavioral response, namely drinking, it may be a function of sensitization of cells in the rostrolateral striatum. SIP may therefore by a product of striatal excitement.

The goal of the following experiments was to test the oral substitution hypothesis as an explanation for sensitized drinking on a restricted food schedule. Both textural and temporal food manipulations were employed in order to increase eating behavior and reduce or abolish SIP. The first study presented food in two distinct forms which take longer to consume than simple pellet food. Drinking is expected to decrease since it will no longer be required as an oral substitute. The second experiment investigated the role of temporal factors in mediating the amount of oral activity required to abolish drinking. Basically, equally sized meals of increasing duration should result in corresponding decreases in water consumption. These meals involved the dispensing of coarse granules previously found to be the minimum diameter required to induce SIP (Mumby & Beck, 1988). Therefore, in controlling for food quantity and texture, this study also makes it possible to assess whether the duration (time) or the quality (texture) of food reinforcement is more important in SIP. The implications of these results will be discussed with respect to the oral substitution hypothesis.

References

Beck, C.H.M., Huh, T.J.S., Mumby, D.G. & Fundytus, M.E. (1989). Schedule-induced behavior in rats: Pellets versus powder. Animal Learning & Behavior, 17(1), 49-62.

Falk, J.L. (1967). Control of schedule-induced polydipsia: Type, size, and spacing of meals. Journal of Experimental Analysis of Behavior, 10, 199-206.

Falk, J.L. (1971). The nature and determinants of adjunctive behavior. Physiology and Behavior, 6, 577-588.

Flory, R.K. (1971). The control of schedule-induced polydipsia: Frequency and magnitude of reinforcement. Learning and Motivation, 2, 215-227.

Freed, W.J. & Mendelson, J. (1977). Water-intake volume regulation in the rat: schedule-induced drinking compared with water-deprivation-induced drinking. Journal of Comparitive and Physiological Psychology, 91, 564-573.

Kenny, J.T., Wright, J.W. & Reynolds, T.J. (1976). Schedule-induced polydipsia: The role of oral and plasma factors. Physiology & Behavior, 17, 939-945.

Mazur, J.E. (1990). Learning and Behavior (2nd ed.). New Jersey: Prentice Hall.

Mumby, D. & Beck, C.H.M. (1988). Schedule-induced polydipsia: Attenuating effects of decreased size of food granulations. Physiology & Behavior, 43, 375-381.

Pisa, M. (1988a). Motor functions of the striatum in the rat: Critical role of the lateral region in tongue and forelimb reaching. Neuroscience, 24, 453-463.

Pisa, M. (1988b). Motor somatotopy in the striatum of rat: Manipulation, biting and gait. Behavioral Brain Research, 27, 21-35.

Poling, A., Krafft, K., Chapman, L. & Lyon, D. (1980). Polydipsia induced by intermittent delivery of salted liquid foods. Journal of the Experimental Analysis of Behavior, 33, 337-344.

Premack, D. (1962). Reversibility of the reinforcement relation. Science, 136, 255-257.

Premack, D. (1963). Prediction of the comparitive reinforcement values of running and drinking. Science, 139, 1062-1063.

Roper, T.J. (1983). Schedule-induced behavior. In R.L. Mellgren (Ed.), Animal cognition and behavior (pp. 127-164). North-Holland Publishing Company.

Rosellini, R.A. & Burdette, D.R. (1980). Meal size and intermeal interval both regulate schedule-induced water intake in rats. Animal Learning & Behavior, 8, 647-652.

Tang, M. & Falk, J.L. (1986). Ethanol polydipsic choice: Effects of alternative fluid polydipsic history. Alcohol, 3, 361-365.

Timberlake, W. & Allison, J. (1974). An empirical approach to instrumental performance. Psychological Review, 81, 146-164.

Wetherington, C.L. & Riley, A.L. (1986). Diminution of schedule-induced polydipsia after a long rest period. Physiology & Behavior, 37, 375-378.

II. Attenuation of Schedule-Induced Polydipsia With Increased Feeding Activity: The Oral Substitution Hypothesis

Rats food deprived to 80% of their preexperimental free- feeding weight drink copious amount of water when food is delivered on an intermittent basis (Falk, 1967). This response is called schedule-induced polydipsia (SIP) and has been studied for almost three decades in an attempt to fully understand the factors that influence it. Despite the robust nature of SIP, especially in rat subjects, there are few theories that can sufficiently explain why this particular adjunctive behavior develops.

One theory of SIP points to prandial drinking as an explanation. According to Roehrs, Allen & Porter (1976), taking a drink after each meal is an innate response that is potentiated with scheduled food delivery. This hypothesis requires that drinking always follow eating in the interfood interval. Unfortunately, research has shown that in longer interfood intervals, drinking tends to have a later onset and therefore does not necessarily immediately succeed food consumption (Segal, Oden & Deadwyler, 1965, cited in Staddon, 1977). SIP has also been attributed to frustration associated with receiving smaller food amounts than would normally be consumed within an interval (Thomka & Rosellini, 1975). The result is energized drinking to excessive levels. This hypothesis falls into the realm of motivational theories which are capable of explaining a number of findings associated with the development of SIP. The major drawback of a frustration explanation, as pointed out by Roper (1983), is that such subjective states are difficult to measure and validate independently of SIP and therefore result in arguments that are circular in nature. Finally, there are the thirst theories which describe polydipsia in physiological terms. There is little support in the literature for such explanations however, since SIP was not found to be mediated by homeostatic controls (Kenny, Wright & Reynolds (1976). Similarly, the data suggesting dry mouth causes SIP are inconclusive since only some liquid diets appear to abolish SIP and salt accounts for the drinking in those that don't (Poling, Krafft, Chapman & Lyon, 1980). The fact that dry powder food cannot sustain SIP settles the argument and discredits the dry-mouth idea (Beck et al., 1989). Perhaps the only contribution the thirst theories make to the study of SIP is their focus on the relationship between feeding and drinking (Roper, 1983). This focus is shared by more recent and more complete explanations of polydipsia - sensitization and the oral substitution hypothesis.

The non-associative learning approach to SIP involves the process of behavioral sensitization (Wetherington & Riley, 1986). The theory proposes that repeated presentation of a stimulus elicits a response which gradually becomes strengthened with time. The response becomes persistent and excessive with each stimulus presentation and fails to occur in its absence. In the SIP paradigm, food is the eliciting stimulus and drinking becomes the sensitized response. This theory adequately accounts for many features of SIP including the fact that it takes several sessions to develop, becomes an exaggerated and persistent response and will not occur when food is no longer presented. The major problem this theory faces is explaining why drinking and not some other food-related behavior is the sensitized response. The solution can be found both behaviorally and anatomically with the oral substitution hypothesis.

A reciprocal relationship between the amount of feeding behavior and drinking has been documented in the literature (Beck, Huh, Mumby & Fundytus, 1989; Reid & Dale, 1983). This finding has led directly to the notion of drinking as an oral substitute for feeding. Essentially, rats given food requiring little oral activity to consume, exhibit excessive drinking in an attempt to substitute for the deprived feeding response. Powder food, on the other hand, fails to induce SIP because it has sufficient levels of feeding behavior and therefore does not require an oral substitute. This oral substitution hypothesis can be considered an extension of the response deprivation theory of reinforcement (Timberlake & Allison, 1974). Feeding is considered a response associated with food reinforcement and occurs at specific levels under normal or baseline meal conditions. When this response is deprived, as with a food reinforcement schedule, other oral behaviors associated with feeding are elicited in an attempt to approach normal consummatory levels. Drinking is the oral substitute in the SIP paradigm when specific food types are delivered.

Anatomically, the oral substitution hypothesis follows logically with the organization of the striatum. According to Pisa (1988a, 1988b), the rostrolateral striatum is specifically involved in orofacial and forelimb movements. Since eating and drinking are both oral behaviors and originate largely from the same brain regions, it is conceivable that if one is restricted, the other will substitute, especially if the cells in the striatum are sensitized. Essentially, polydipsia could be a product of striatal excitation.

The main purpose of the present study was to test the oral substitution hypothesis with two different food manipulations, each designed to increase the amount of feeding. The expected outcome would be a cancellation of polydipsia since these food types, although equal in amount to pellets, do not lead to deprivation of the feeding response. Drinking will no longer be required as an oral substitute. In addition to decreased drinking levels, a negative relationship between feeding and drinking is expected in accordance with previous work (Beck et al., 1989). The types of oral activity associated with food consumption were also examined in an attempt to examine this eat-drink relationship more closely. Based on an earlier study (Mumby & Beck, 1988), it is expected that eating will be the principal oral behavior to show this inverse relationship to drinking. In addition, several non-oral ambulatory behaviors were analyzed in order to assess any changes in general activity levels across food conditions. Certain activities may drop out of the behavioral repertoire when feeding is increased, while others remain. The results of this investigation will contribute to the understanding of SIP and the oral substitution hypothesis proposed to explain it.

Methods

Subjects

The subjects were 14 male Sprague Dawley rats (University of Alberta, Ellerslie) weighing 250-395 g at the beginning of the experiment. The animals were housed individually in clear plastic cages under a 12:12 hr light- dark cycle with lights on at 0700. Colony room temperature was maintained at 22 (+/- 1) °C with 51% humidity. Water, but not food, was available ad libitum in the home cage.

Apparatus

A 20 x 23 x 23-cm opaque box was designed with a transparent Plexiglas front wall and ceiling. This test chamber included a 3 x 3.5

x 2-cm deep feeder cup fixed to a wall 6 cm above the floor. Food was delivered automatically from a pellet dispenser or manually through a 1.5 cm diameter tube into the feeder cup. A water spout protruded 1 cm into this same wall 3 cm above the top of the feeder cup. The spout was connected to a 50-ml burette. Testing occurred in a dimly illuminated room (red light) accomplished by covering the overhead fluorescent lights with red Mylar film. Background noise at 65 dB SPL was supplied by an electric fan during all experimental sessions.

Procedure

Prior to testing, each animal was food deprived to 80% of its preexperimental free-feeding weight over a two week period. During this time, the subjects were handled and weighed on a daily basis. Reduced body weight was maintained throughout the experiment with daily meals of Purina Rat Chow. Upon reaching their assigned weights, the animals began the 14 session experimental program which included three food conditions. Pellets (Bio Serv, 45 mg) were administered on Sessions 1-10 as part of the polydipsia training, and again on Sessions 12 and 14. Sessions 11 and 13 involved delivery of two other food types. Pit consisted of a single pellet surrounded by a mixture of equal amounts of paraffin and black sand. The resultant ball was approximately 10-12mm in diameter. Shell, on the other hand, was made by rolling an 8-mm paraffin coated bead in crushed pellets. All conditions had the same quantity of nourishment (45 mg +/- 0.04, mean +/- SE) and were delivered on an FT 60-s schedule of food reinforcement. Random assignment to one of two groups determined which food treatment was given first. Group P-S (n = 7) was administered pit food in Session 11 and shell in Session 13 while the reverse order was applied to Group S-P (n = 7). Manual delivery of pit and shell was accompanied by the sound of the solenoid used to operate the pellet dispenser. Testing was conducted 5 days a week between 0900 and 1400.

Measures

On each of the 14 testing sessions, the amount of water consumed by each animal was recorded to the nearest 0.1 ml. Sessions 10-14 included additional behavioral measures coded by microcomputer from videotape. For each 50-min session, coding was divided into four, 5-min trials. Trial 1 began at the start of the session and was followed by subsequent trials at intervals of 10 min. Each key press represented a specific behavior which was recorded with the time of entry. In total, 12 behaviors were coded as mutually exclusive categories. These included: food uptake, taking food into mouth; chew, jaw movements with mouth full; bite, biting anything but the food or itself; lick, tongue movements directed at anything but food, water or itself; lick drink, lapping up water splashed into the chamber; drink, drinking water from the spout; groom, scratching, biting, washing and/or licking itself; forepaw action, rapid back and forth movements of the forelimbs, mostly directed at the water spout, feeder cup or corners of chamber; rear, raising forelimbs above feeder cup level; locomote, moving forequarters into one of the four quadrants of the test chamber; immobile, sitting or lying with no movement of any body part; investigate, any movement not involved in the other behavioral categories including mostly sniffing of chamber area. Both intertest and interjudge reliability were assessed for this behavioral coding procedure revealing greater than 80% agreement on all measures across selected sessions.

Data analysis included quantification of each of the aforementioned behaviors. Essentially, each occurrence of a behavior was defined and analyzed as a bout of that behavior. Three measures were completed: percent time (PT), the percent of total trial dedicated to a behavior; bout frequency (BF), the number of bouts of a specific behavior within a trial and bout duration (BD), the transformed mean duration of bouts of a behavior in a given trial. The transformation was calculated in order to normalize these data and involved taking the square root [1 plus the mean BD in s]. Repeated measures of conditions, sessions and/or trials ANOVA were applied to each measure of each behavior (except when it occurred less than 1% of the time). Heterogeneity of covariance was corrected for by applying the Geisser Greenhouse correction factor (ϵ = 1/t- 1). Significant ANOVA's were subjected to both Newman-Keuls multiple comparisons and correlation analysis ($p<.05$), where appropriate.

Results

For the 10 days of pellet training, ANOVA of the volume of water drunk showed a significant sessional effect, $F(9,117) = 41.04$, $p<.005$ (Figure II-1). There was no difference between Sessions 1 and 2 but drinking progressively increased from Session 2 to Session 5 (Newman-Keuls). The last five days of training did not differ in volume consumed. For this as well as for other measures to be discussed, ANOVA revealed no significant order effects between sessions within the pit and shell conditions. Consequently, the sessional data were collapsed into one pit and one shell set of scores. These data are presented as the pit and shell conditions in the figures and text. One- way ANOVA with condition as the repeated measure (Session 10, 12, 14, pit and shell) revealed a significant effect for water volumes, $F(4,52) = 116.86$, $p<.005$. No differences were found between the three pellet sessions but the subjects drank more water in this condition than in both pit and shell. In addition, Figure II-1 shows pit sessions had significantly higher volumes than shell sessions.

In order to understand the relationship between drinking and feeding, several oral behaviors were analyzed across the three food treatment conditions. The results of the significant one-way ANOVA's for the PT measure of these behaviors are represented graphically in Figure II-2. Essentially, food uptake was found to occur more often during pit and shell sessions compared to pellet, $\underline{F}(4,52) = 190.33$, $\underline{p}<.005$. When drinking was considered however, the opposite trend was found. Across conditions, drink was significantly excessive in all three pellet sessions in contrast to pit and shell, $\underline{F}(4,52) = 71.1$, $\underline{p}<.005$. The three remaining oral behaviors illustrated in Figure II-2 basically replicated this same pattern. Chew, bite and groom were significant across conditions, $\underline{F}(4,52) = 7.18$, $\underline{p}<.025$; $\underline{F}(4,52) = 5.52$, $\underline{p}<.05$; $\underline{F}(4,52) = 5.49$, $\underline{p}<.05$, respectively, but bite was the only behavior with higher scores in pellet compared to <u>both</u> pit and shell. For chew, pellet only exceeded shell while groom only showed pellet greater than pit. The two categories of lick and lick drink failed to show any significance when analyzed for condition effects.

Based on these PT data, food uptake and drink were further analyzed on the BF and BD measures for a more complete behavioral description. Because no significant differences were found for the three pellet sessions 10, 12 and 14, these data were collapsed. One-way ANOVA's documented significant condition effects for both measures of these oral behaviors, as shown in Figure II-3. Food uptake revealed pit and shell were greater than pellet for both BF, $\underline{F}(2,26) = 20.56$, $\underline{p}<.005$, and BD,

$F(2,26) = 305.66$, $p<.005$. On the other hand, drink BF, $F(2,26) = 16.48$, $p<.05$, and BD, $F(2,26) = 19.83$, $p<.05$, were significant with pellet sessions having higher scores than pit and shell. In essence, the BF and BD scores for food uptake and drink describe the same trends found for PT. In summary, bouts of food uptake were more frequent and of longer duration during pit and shell thereby contributing to the higher percentage of time spent engaged in this activity during these food conditions compared to pellet. The opposite case can be described for drink since bouts of drinking were shorter and less frequent in pit and shell sessions than in pellet.

In comparing the pit and shell conditions with each other, some significant findings with respect to the oral behaviors were found (Newman-Keuls multiple comparisons). Essentially, subjects devoted more time to food uptake during pit sessions in contrast to shell (PT scores, Figure II-2). BF revealed higher values for shell for food uptake, but the opposite trend was reported for BD of food uptake and drink. Pit food therefore involved more oral activity because the food took more time to eat and drinking bouts were longer than in the shell condition.

The data presented thus far illustrate several trends regarding both the level of drinking and the amount of oral activity across conditions. To summarize, pit and shell food was associated with low drinking volumes but high measures (PT, BF and BD) of food uptake behavior compared to pellet. The reduced level of water intake was paralleled by the behavioral category drink which occured less often during pit and shell than in pellet (PT, BF and BD). Chew, bite and groom followed a similar trend with smaller PT scores in either or both of pit and shell sessions compared to those where pellet food was delivered. In order to further highlight the relationships between drinking and these significant oral behaviors, correlations on the PT scores were performed for all 14 subjects. The behavior drink was found to be negatively correlated with food uptake across all food conditions ($r = -.82$, $p<.005$). The same results were found when drinking volumes were compared to food uptake scores ($r = -.84$, $p<.005$), as expected. Additional correlations confirmed the finding of similar patterns of drinking compared to the remaining oral behaviors - chew ($r = .55$, $p<.025$), bite ($r = .45$, $p<.05$) and groom ($r = .37$, not significant). All three of these behaviors were positively correlated with drinking thereby suggesting that the only significant oral activity to be inversely related to drinking was food uptake.

The various oral behaviors were also examined across trials in order to document activity within each food condition. Pellet sessions 10, 12 and 14 were collapsed for one-way ANOVA with trials as the repeated measure. The only oral behaviors to exhibit significant effects were food uptake and drink (Figure II-4). Other behaviors failed to do so (data not shown). The pellet condition revealed Trial 1 exceeded all other trials for PT of food uptake, $F(2,26) = 11.02$, $p<.01$. Drink, on the other hand, was once again found to have the opposite trend since Trial 1 was significantly lower than Trials 2, 3 and 4, $F(2,26) = 13.26$, $p<.005$. BF and BD measures of these respective behaviors paralleled the PT findings for pellet, although only BD reached significance, $F(2,26) = 6.8$, $p<.025$; $F(2,26) = 8.91$, $p<.025$.

With respect to the pit and shell food treatments, only the pit condition demonstrated significant effects for food uptake and drink. Again, none of the other oral behaviors revealed a trials effect (data not shown). PT spent engaged in food uptake was greatest in Trial 1 compared to the remainder of the session, $F(2,26) = 44.91$, $p<.005$. As in the pellet condition, drink PT scores were significantly lower in Trial 1 compared to Trials 3 and 4, $F(2,26) = 6.95$, $p<.025$. Analysis of BF and BD for these oral behaviors once again replicated their respective PT findings. Food uptake BF, $F(2,26) = 8.18$, $p<.025$, but not BD, was significant while both BF and BD measures were significant for drink, $F(2,26) = 8.96$, $p<.025$; $F(2,26) = 5.78$, $p<.005$, respectively. In summary, analysis across trials revealed that for pellet and pit food types, the subjects spent more time engaged in food uptake and less time drinking in Trial 1 compared to any other segment of the session. For pellet, food uptake was also of longer duration in the early part of the session in contrast to shorter bout durations of drink. Pit food differed in this respect since only the frequency of food uptake was highest in Trial 1 while both frequency and duration of drink were decreased in this segment compared to the rest of the session. In addition, overall Trial 1 drink versus food uptake revealed a negative correlation for both the pellet and pit conditions, but these values did not reach $p<.05$ significance.

Of the five remaining coded behaviors, immobile was not analyzed because it occurred less than 1% of total trial time. All pellet sessions were collapsed and compared to pit and shell in two-way ANOVA's with repeated measures for conditions and trials. These data are depicted in Table II- 1 and Figure II-5. Condition effects were significant for PT investigate, $F(1.8,24) = 8.69$, $p<.005$, and PT forepaw action, $F(1.6,21.2) = 15.78$, $p<.005$. For investigate, subjects spent less time engaged in this behavior during pit food delivery than pellet. Forepaw action, on the other hand, was lower in <u>both</u> of the two treatment conditions compared to pellet sessions. This finding is interesting in that it paralleled the pattern found fo the oral behaviors drink, chew, bite and groom. Pit and shell therefore had less time devoted to investigatory activity and forepaw action in much the same fashion as the non-eat oral behaviors, compared to pellet. Rear and locomote PT scores were not found to demonstrate a significant condition effect and therefore did not change with food manipulation (Table II-1).

Analysis over trials found significance for forepaw action only, $\underline{F}(1.2,15.8) = 4.98$, $\underline{p}<.05$ (Figure II-5). Condition x Trials interactions were revealed for investigate, $\underline{F}(3.8,49.5) = 7.35$, $\underline{p}<.005$ and locomote, $\underline{F}(3.7,47.9) = 3.71$, $\underline{p}<.02$ but not rear or forepaw action. As illustrated in Figure II-5, multiple comparisons of these general activity behaviors disclosed some significant trends. For investigate, Trial 1 was lower than Trials 2, 3 and 4 during the pit condition. Locomote constituted more time in Trial 1 during pellet delivery but was lowest compared to Trial 4 when pit food was administered. Finally, forepaw action was lowest in Trial 1 compared to the remaining trials in both pellet and pit conditions, a trend which once again fully replicates that seen for drinking. As before, no trends were found during shell sessions. In summary, subjects engaged in more locomote and investigate (nonsignificant trend) during Trial 1 of the pellet condition and less of these behaviors during Trial 1 of the pit condition.

Discussion

Before delivery of the pit and shell food types, all subjects showed polydipsic levels of drinking. Water consumption increased gradually over the first five sessions and, at asymptote, was greater than four times that measured on Session 1 (see also Falk, 1971; Mumby & Beck, 1988). In addition, as reported by Cook et al. (1983), the total volume of water drunk on the last day of polydipsia training was approximately equal to 10 ml for every g of food consumed. If these measures are applied to water levels consumed during either of the pit and shell conditions, it is obvious that drinking did not differ from initial training sessions and only amounted to 2.3 and .86 ml of water per g of pit and shell food, respectively. In other words, SIP was absolutely cancelled on those days when pit and shell were given instead of pellets. The robustness of SIP was demonstrated by its return to asymptotic water levels when pellets were again delivered on the baseline days in between. Polydipsia was essentially interrupted by food presented in a different form or texture than pellets.

In addition to the principal finding of a four-fold reduction in water volume consumption with food requiring extensive oral activity, the results of this study also describe a reciprocal relationship between feeding and drinking. The act of taking food into the mouth was the critical oral behavior found to be negatively correlated with both the behavior drink and the volume of water consumed. During pellet sessions, food uptake was quick and thereby constituted less time during the session. Consequently, drinking volumes were high. Pit and shell, on the other hand, had frequent bouts of food uptake that were of long duration--hence water volumes were normal. All other oral behaviors that showed any significant effect of condition (drink, chew, bite, groom) had effects opposite to food uptake. Since food manipulation was the main factor designed to increase the time spent engaged in oral activity, these findings are important. It appears that all other oral behaviors, including drink, occur more often in pellet sessions because food uptake is so efficient. When food uptake is deliberately prolonged, bite, chew, groom and even forepaw action join with drink in dropping out of the behavioral repertoire, possibly because they are no longer required as oral substitutes. The inclusion of forepaw movements with these oral behaviors is not surprising in light of the fact that forelimb and orfacial movements, including tongue protrusions have been mapped in the same brain region--the rostrolateral striatum (Pisa, 1988a; Pisa, 1988b). In fact, this finding supports the notion of striatal excitement in SIP and follows with the anatomical expectations of the oral substitution hypothesis.

When trials within each condition are considered, food uptake is again the one oral behavior in direct opposition to all others, including drink. During pellet sessions, drink and food uptake were the only oral behaviors to reveal a trials effect. Trial 1 had less drinking (PT, BF and BD) but more time devoted to food uptake (PT, BD) than Trials 2, 3 and 4. Essentially, pellet food was consumed faster after Trial 1 and drinking behavior subsequently increased. This lends further credence to the reciprocal relationship between drinking and oral activity associated with feeding. The pit condition did not differ from pellet with respect to individual oral trials effects except to add bite and groom. Again, food uptake showed the opposite trend to all other behaviors, including drink.

Based on the aforementioned data, it can be said that food uptake is the critical oral variable in producing the inverse relationship with drinking level (and drinking behavior) across all conditions. This finding not only supports the oral substitution hypothesis but also replicates the report of head in feeder (a category equivalent to food uptake in this study) as the only behavior to exhibit this reciprocal relation with drinking (Mumby & Beck, 1988).

Several factors need to be discounted as contributing to the effects described herein. Procedural differences were circumvented by using the same test chambers and machinery for each type of food delivery. Even though pit and shell were administered manually, the pellet dispenser solenoid was operational as a timing device throughout these sessions. Satiation can also be discounted as a factor since the amount of food delivered was controlled for across food types. Similarly, any salient feature of the food with respect to flavor, moisture content or nutritional quality is of minimal influence since pellet and pit were of the same name brand and shell was made from crushed pellets. Analysis of all behaviors other than drink or food uptake refutes the suggestion of the subjects engaging excessively in some other activity which might compete with the polydipsic response. Essentially, no differences were found for general activity levels (i.e., investigate, locomote, rear) across conditions and pit and shell had fewer occurrences of oral behaviors (except food uptake) compared to pellet. Based on these data, one can also dismiss the possibility that SIP was, in effect, cancelled during pit and shell because of decreased levels of arousal or activity compared to pellet sessions. Finally, and most importantly, the notion of interfood interval needs to be assessed with respect to pit and shell food delivery. It may be argued that by increasing the time required to consume food within the same FT 60-s schedule of delivery effectually serves to reduce the perceived interfood interval. However, SIP has been described with FT schedules as short as 15 s (Poling et al., 1980). Previous work measuring this parameter (with pellet food) has also found reduced levels of drinking at short interpellet intervals (ipi) (Flory, 1971; Falk, 1967). Reduced levels of drinking (i.e., nonoptimal polydipsia) is not the same as a return to initial drinking levels and below (i.e, nonpolydipsic) as was found in this study. Consequently, any perceived change in the interfood interval by the rats in this experiment can be said to have a negligible effect on drinking behavior.

The nullification of SIP with the food manipulations in the present investigation cannot be explained by these factors relating to food quality, experimental procedure or temporal variables. The differences in drinking levels between pit and shell however, do suggest that the form in which food is presented may be a significant influence. Remember that the pit food was a hard pellet center in a ball of wax while shell was a powder coated bead. More drinking occurred in pit compared to shell which, although not polydipsic, suggests that the pellet may induce more of a drinking response than powder. The influence of food texture on drinking is not unknown since the literature reports SIP with pellets and coarse food but not with fine granules (Mumby & Beck, 1988), powder (Beck et al., 1989) or liquid (Poling et al., 1980; Stein, 1964). The type of food reinforcement may therefore be said to influence the amount of feeding activity and the resultant requirement for drinking as an oral substitute.

The fact that the pit and shell food types differed in form and texture not only influenced drinking but also affected food uptake behavior. The pit food had more time devoted to feeding compared to shell. More specifically, with pit food, the animals had longer durations of food uptake compared to pellet and shell because the wax coating had to be removed before the food inside could be consumed. Shell, on the other hand, had more frequent bouts of food uptake than pellet or pit because the animal had access to previous beads during the interfood interval. After eating the powder from the wooden bead, it was often the case that another bead was picked up from the floor of the test chamber and manipulated for possible remnants of powder to eat. In sum, pit had higher drinking volumes than shell and had lower BF scores for feeding. These findings suggest that within the pit and shell treatments, only the bout frequency of food uptake is reciprocally related to drinking levels, not bout duration. This observation qualifies the fact that PT for feeding in these treatments does not support the oral substitution hypothesis.

The data presented herein can also be discussed in terms of the various theories of SIP. Frustration theory would predict that drinking levels would not change since in each food treatment, the subjects received the same small amount of food (Thomka & Rosellini, 1975). In other words, pit and shell should still show the same energized drinking response. These data do not fit with a frustration explanation. On a similar vein, thirst theories fail to account for the findings of this experiment since they would predict equal amounts of drinking across food treatments. Dry-mouth has been proposed as an explanation for pellet induced drinking (Stein, 1964) yet volume of water consumed is considerably reduced with pit and shell despite the fact that no difference in moisture content exists between these food conditions and pellets. Adventitious learning has been discounted as a viable explanation for SIP (Staddon, 1977) and is also unable to account for the findings of this pit and shell study. This theory proposes that food arrival superstitiously rewards normal drinking in the early sessions.

A contiguous relationship develops between the two oral behaviors and drinking thereby becomes excessive. The major problem with such an explanation is an inability to specify why drinking is the behavior adventiously reinforced by food. In the early sessions, several activities have an equal opportunity to become contiguous with food delivery, but SIP is always the resultant response when water is available. In addition, adventitious learning cannot explain why polydipsic rats no longer drink when food of a different type is presented on the same schedule. Finally, unlike these previous theories, the sensitization theory, in combination with the oral substitution hypothesis, is able to account for the data in this investigation. According to Wetherington and Riley (1986), repeated presentation of food serves to elicit the drinking response. In this experiment, pellet food sensitized drinking to polydipsic levels. Drinking therefore became the oral substitute for restricted eating behavior, as predicted by the oral substitution hypothesis. When pit and shell food was administered, the sensitized animal no longer responded with drinking possibly because the form and texture of the food sufficiently altered its properties as an eliciting stimulus.

In summary, this experiment supports the oral substitution hypothesis as an explanation of drinking as the sensitized response in SIP. Future research could extend and improve the data collected here with an analysis of behavior within the interfood interval as well as within the session. This information would reveal when drinking occurred in pit and shell to see if it was still somewhat related to feeding (i.e., occurs directly after food consumption). Further studies designed to increase the amount of feeding behavior with other food manipulations (meal duration) may also strengthen the notion of oral substitution as an important factor in the development of SIP.

Table II-1

Mean and SE of PT Scores Across Food Conditions for General Activity Behaviors

Behavior		Condition		
		Pellet	Pit	Shell
Investigate	*M*	47.94	36.23*	43.76
	SE	1.66	1.42	1.84
Locomote	*M*	3.60	3.14	3.33
	SE	0.17	0.21	0.21
Rear	*M*	2.99	2.11	3.15
	SE	0.41	0.43	0.56
Forepaw Action	*M*	10.28	3.29*	4.18*
	SE	0.87	0.87	0.57

*$p < .05$ significance from pellet condition

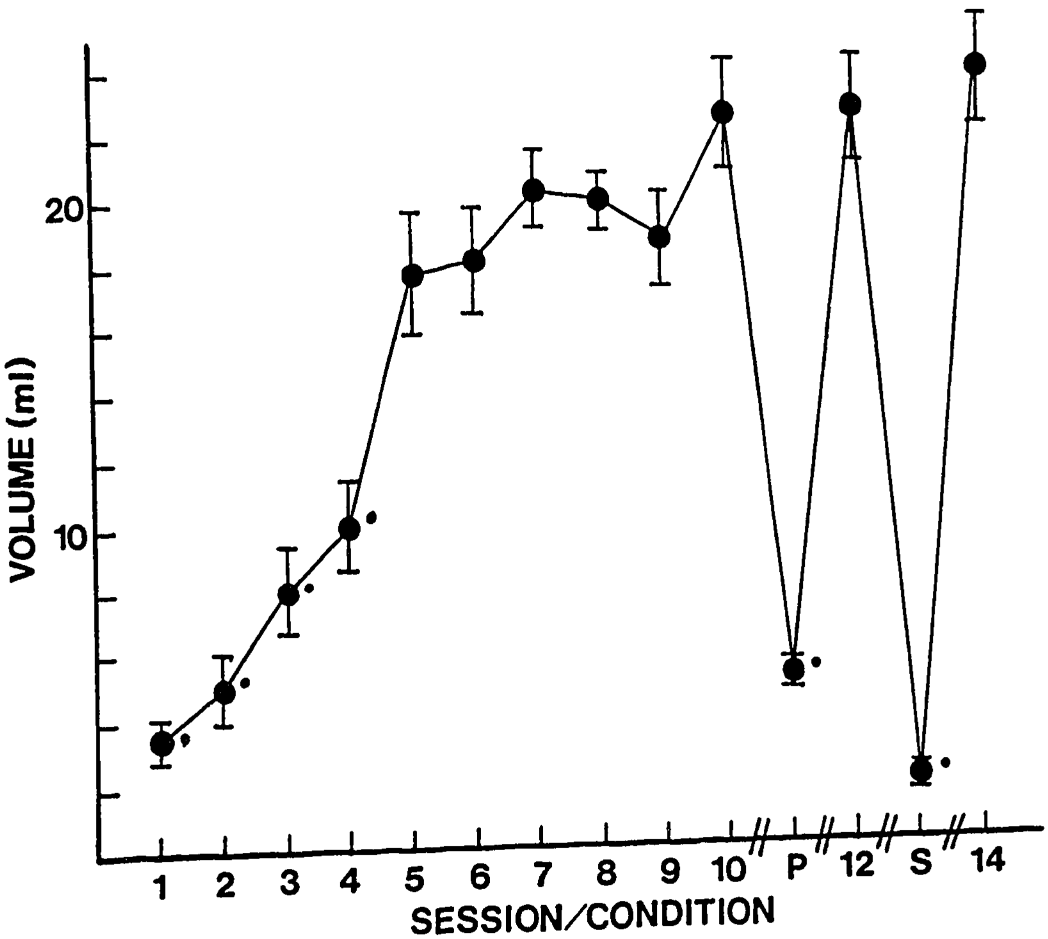

Figure II-1: Volume of water consumed during polydipsia training and pit and shell treatments. Dots denote significant difference from means of Sessions 10, 12 and 14, $p<.05$.

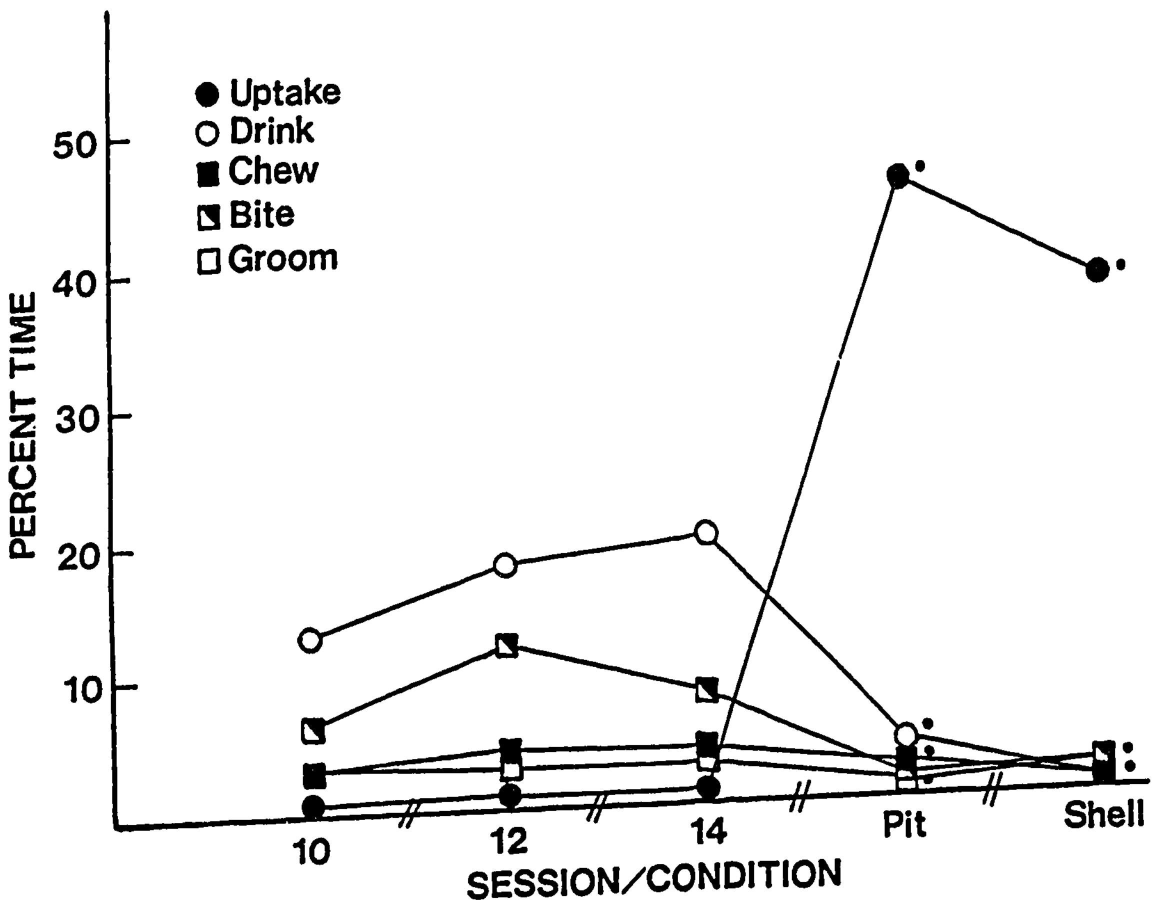

Figure II-2: PT for food uptake, drink, chew, bite and groom across pellet Sessions 10, 12, 14 and pit and shell. Dots denote significant difference from means of Session 10, 12 and 14, $p<.05$.

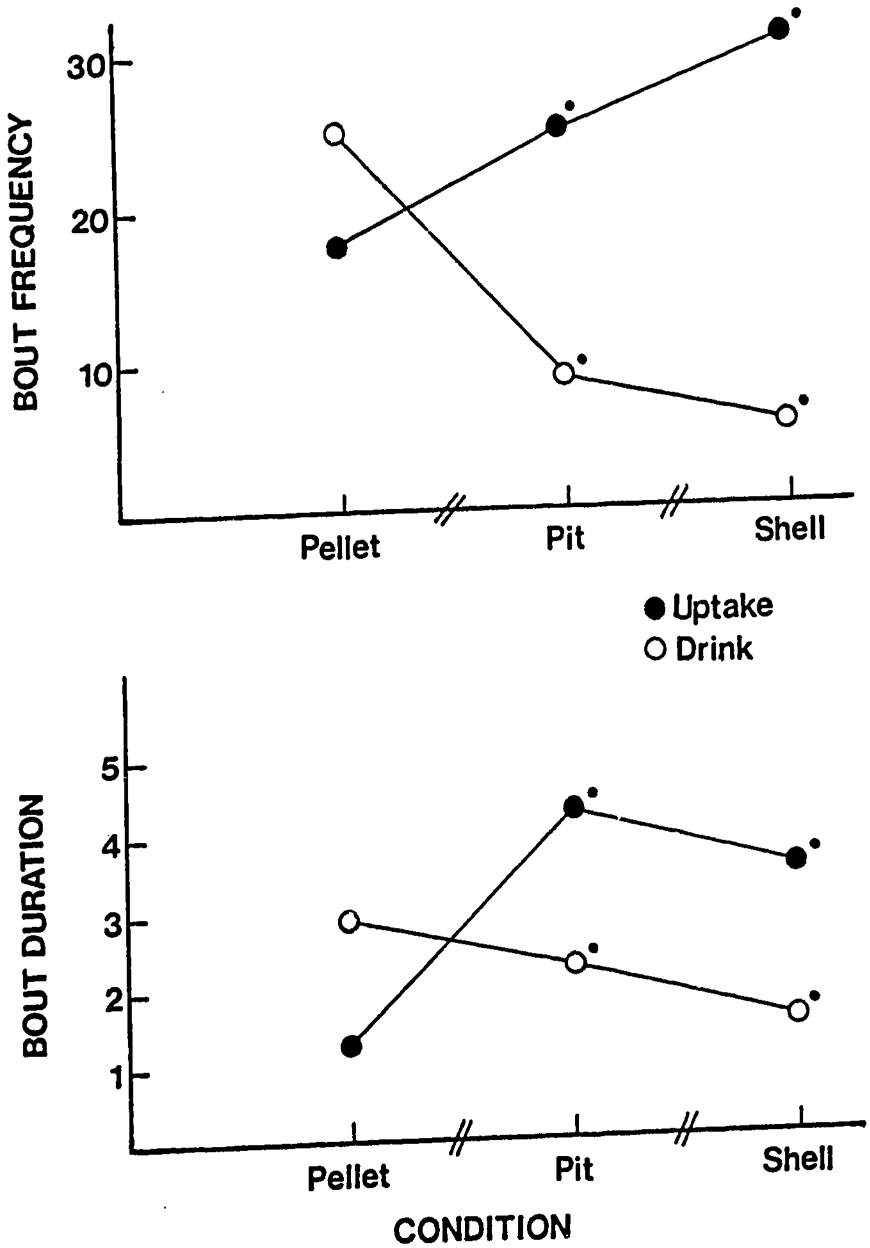

Figure II-3: BF and BD for food uptake and drink across pellet (Sessions 10, 12 and 14 collapsed), pit and shell. Dots denote significant difference from pellet mean, $p<.05$. SE's are less than 15% of group means.

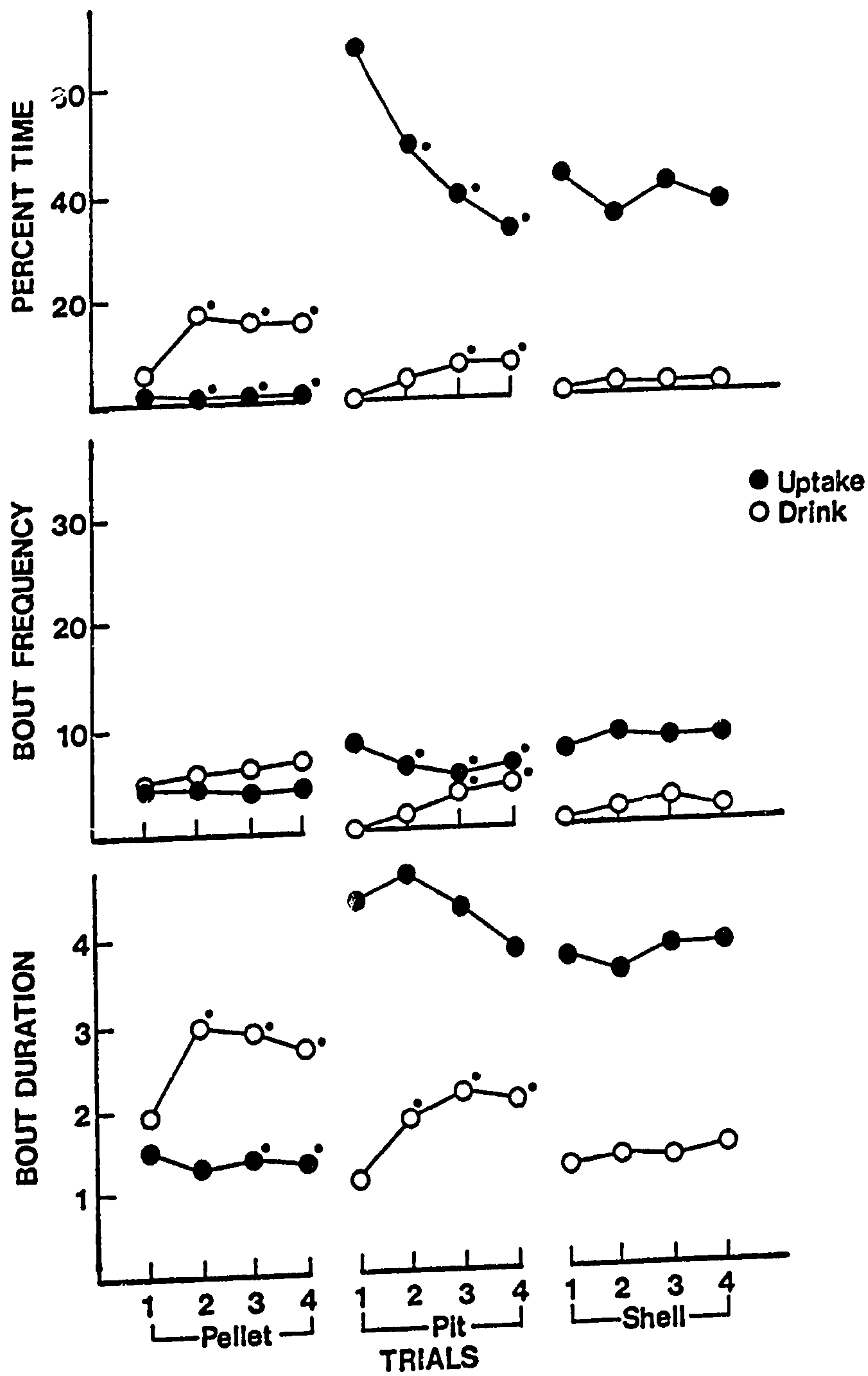

Figure II-4: PT, BF and BD for food uptake, and drink across trials in each condition. Pellet Session 10, 12 and 14 were collapsed. Dots denote significant difference of means from Trail 1 in each condition, $p<.05$. SE's are less than 20% of group means.

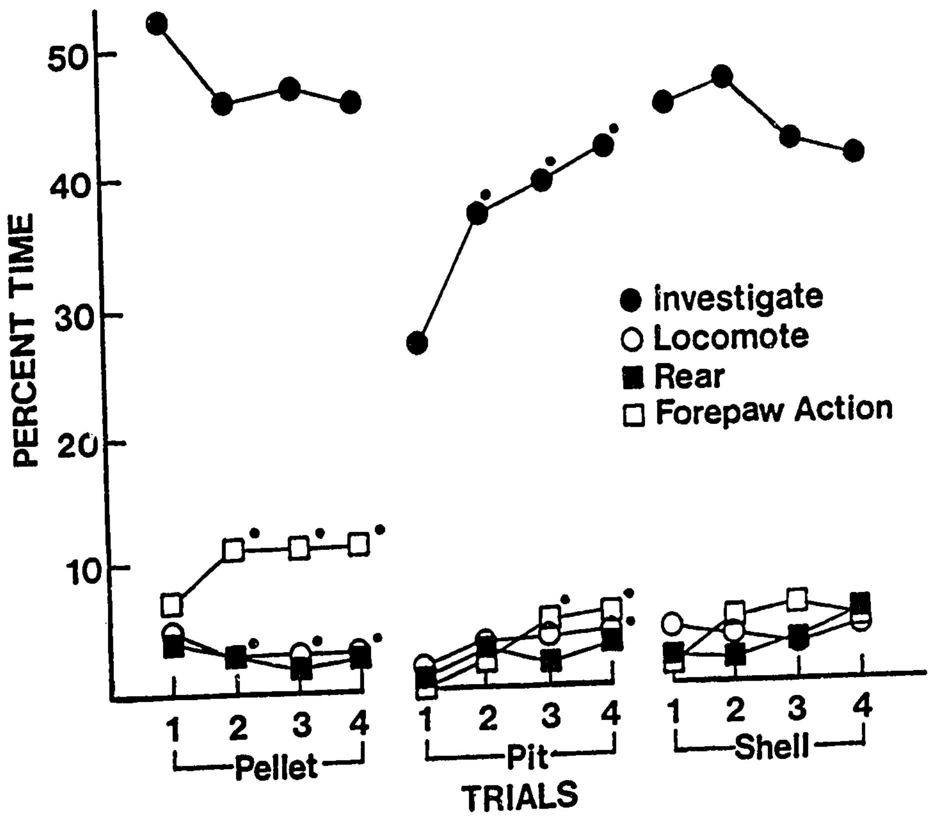

Figure II-5: PT for investigate, locomote, rear and forepaw action across trials in each condition. Pellet Sessions 10, 12 and 14 were collapsed. Dots specify significant difference from Trial 1 means in each condition, p<.05. SE's are less than 20% of group means.

References

Beck, C.H.M., Huh, T.J.S., Mumby, D.G. & Fundytus, M.E. (1989). Schedule-induced behavior in rats: Pellets versus powder. Animal Learning & Behavior, 17(1), 49-62.

Cook, P., Wallace, M. & Singer, G.A. (1983). A reinterpretation of schedule-induced behaviors based on a systematic analysis of behavior. Neuroscience & Biobehavioral Reviews, 7, 97-104.

Falk, J.L. (1967). Control of schedule-induced polydipsia: Type, size, and spacing of meals. Journal of Experimental Analysis of Behavior, 10, 199-206.

Falk, J.L. (1971). The nature and determinants of adjunctive behavior. Physiology and Behavior, 6, 577-588.

Flory, R.K. (1971). The control of schedule-induced polydipsia: Frequency and magnitude of reinforcement. Learning and Motivation, 2, 215-227.

Kenny, J.T., Wright, J.W. & Reynolds, T.J. (1976). Schedule-induced polydipsia: The role of oral and plasma factors. Physiology & Behavior, 17, 939-945.

Mumby, D. & Beck, C.H.M. (1988). Schedule-induced polydipsia: Attenuating effects of decreased size of food granulations. Physiology & Behavior, 43, 375-381.

Pisa, M. (1988a). Motor functions of the striatum in the rat: Critical role of the lateral region in tongue and forelimb reaching. Neuroscience, 24, 453-463.

Pisa, M. (1988b). Motor somatotopy in the striatum of rat: Manipulation, biting and gait. Behavioural Brain Research 27, 21-35.

Poling, A., Krafft, K., Chapman, L. & Lyon, D. (1980). Polydipsia induced by intermittent delivery of salted liquid foods. Journal of the Experimental Analysis of Behavior, 33, 337-344.

Reid, A.K. & Dale, R.H.I. (1983). Dynamic effects of food magnitude on interim-terminal interaction. Journal of the Experimental Analysis of Behavior, 39, 135-148.

Roehrs, T., Allen, J.D. & Porter, J.H. (1976). Acquisition of schedule-induced polydipsia in rats with no prior drinking experience. Physiology & Behavior, 17, 1011-1013.

Roper, T.J. (1981). What is meant by the term "schedule-induced," and how general is schedule induction? Animal Learning & Behavior, 9, 433-440.

Roper, T.J. (1983). Schedule-induced behavior. In R.L. Mellgren (Ed.), Animal cognition and behavior (pp. 127-164). North-Holland Publishing Company.

Staddon, J.E.R. (1977). Schedule-induced behavior. In W.K. Honig & J.E.R. Staddon (Eds.), Handbook of Operant Behavior (pp. 125-152). NJ: Prentice-Hall.

Stein, L. (1964). Excessive drinking in the rat: Superstition or thirst? Journal of Comparitive & Physiological Psychology, 58, 237-242.

Thomka, M.L. & Rosellini, R.A. (1975). Frustration and the production of schedule-induced polydipsia. Animal Learning & Behavior, 3, 380-384.

Timberlake, W. & Allison, J. (1974). An empirical approach to instrumental performance. Psychological Review, 81, 146-164.

Wetherington, C.L. & Riley, A.L. (1986). Diminution of schedule-induced polydipsia after a long rest period. Physiology & Behavior, 37, 375-378.

III. Maintenance of Schedule-Induced Polydipsia With Increasing Granule Meal Durations

The phenomenon of schedule-induced polydipsia (SIP) was first described by Falk (1961, cited in Roper, 1983) as excessive drinking resulting from intermittent food delivery in food deprived rats. Since this discovery, various factors known to influence SIP have been examined extensively. Varying the schedule of food delivery, for example, has been found to produce a bitonic function of fluid intake (Falk, 1967; Flory, 1971). Essentially, optimal levels of SIP are produced with an interpellet interval (ipi) between 60 and 180 s. Schedules with temporal parameters outside this range do not induce a strong polydipsic response, at least with one pellet per food delivery. Reinforcement magnitude has been shown to interact with the ipi since increases in meal size sustained SIP at ipi's much greater than 180 s (up to 720 s) (Rosellini & Burdette, 1980). Larger pellet meals (i.e., >1 pellet) can also produce increased drinking above small meals at fixed time (FT) 120 s (Yoburn & Flory, 1977). With this particular schedule of food reinforcement however, these authors report no further increase in fluid consumption with meals larger than 2 pellets. More recent studies have focused on food type and SIP. Pellets were the first form found to produce SIP but, according to Mumby and Beck (1988), coarse food texture is the minimum requirement. These authors varied the diameter of the food granules delivered on an FT 60-s schedule of reinforcement and found that drinking increased with particle size. Powdered food (Beck, Huh, Mumby & Fundytus, 1989; Mumby & Beck, 1988) and unsalted liquid (Poling, Krafft, Chapman & Lyon, 1980) do not produce copious drinking when delivered on an intermittent schedule.

From a theoretical point of view, SIP has been subjected to a variety of explanations. The sensitization approach to SIP describes excessive drinking as a sensitized response resulting from repeated presentations of the food stimulus (Wetherington & Riley, 1986). This theory adequately explains many features of SIP including its gradual development, persistence, excessiveness and absence when food is no longer delivered. A second theoretical approach to SIP compliments this sensitization process in outlining why drinking is the elicited response on a food deprivation schedule. Essentially, the oral substitution hypothesis proposes that drinking will substitute for restricted feeding with food requiring little oral activity to consume. The fact that drinking is elicited by the presentation of food follows logically both from a behavioral and an anatomical perspective. According to response deprivation theory, restricted feeding can act as a reinforcer for other behaviors within the same general class (Timberlake & Allison, 1974). Drinking is therefore an oral substitute for eating if this behavior is restricted by the food schedule or the form in which it is presented. This reciprocal relationship between feeding and drinking has been documented previously in the literature (Beck et al., 1989; Reid & Dale, 1983). Both of these studies showed that time spent in the feeder was inversely related to time spent drinking. The first study manipulated food texture to increase feeding while the second varied the amount of reinforcement delivered. These data suggest that various food manipulations can influence feeding behavior to reduce response deprivation within the food schedule and subsequently decrease drinking as an oral substitute. With respect to the anatomical origin of these consummatory behaviors, the rostrolateral striatum has been mapped and identified as having a major role in orofacial movements (Pisa, 1988a, 1988b). If this area of the brain is sensitized, it is not surprising that drinking substitutes for eating since these activities involve similar oral and facial gestures.

The primary purpose of the present experiment was to further test this oral substitution hypothesis with temporal food manipulation. If the amount of oral feeding behavior is the key to SIP, it follows that extending the duration of a meal of coarse granules previously found to induce SIP should, in effect, decrease drinking in a reciprocal fashion. More specifically, forcing rats to eat a coarse meal for 0, 14, 21 or 28 s should progressively increase the amount of feeding behavior and, according to the oral substitution theory, result in a corresponding decrement in water intake. These meal durations were chosen to cover the range of time required to consume both pellet and powder food for comparison with granule food. These three food types were delivered in a within-subjects design with subjects as their own controls. An ethological analysis of specific oral behaviors in addition to eating and drinking was included in an attempt to document which activities fall into the realm of feeding behavior. Previous work has suggested that head in feeder is the only eating behavior to show a negative correlation with drinking (Mumby & Beck, 1988), but with a different food treatment, this finding may be expanded to include additional oral activities. General activity levels were also analyzed across food conditions in order to assess which of these behaviors decreased with increased meal duration. It is expected that the subjects will have less time to spend exploring with each increase in time devoted to feeding. The results of this investigation will contribute to a further understanding of SIP and the variables that control it.

Methods

Subjects

The 14 male Sprague Dawley rats (University of Alberta, Ellerslie) were approximately 7 weeks old and weighed 300- 395 g upon receipt from animal services. All animals were housed singly in clear plastic cages in a colony room maintained on a 12:12 hr photoperiod (lights on at 0700). Room temperature was normal at 22 (+/- 1 °C) and humidity measured 51%. Free access to water was available in the home cage, but food was restricted.

Apparatus

Testing was completed in an opaque box measuring 21.5 x 23 x 23 cm with a Plexiglas front wall and ceiling. One side wall was designed to accommodate either of two feeder cups, depending on the experimental condition. Pellet food (Noyes, 45 mg) was delivered by a pellet dispenser (Coulbourn Instruments) into a 3 x 3.5 x 2-cm deep tray fastened 6 cm above the chamber floor. Purina rat chow, crushed and sifted to 0.8-1.0 mm size particles, was discharged from a motor driven (Princeton Industries) powder trickler (Omark Industries). The trickler was rotated at various speeds to ensure that each meal was of the same mass and only the duration of arrival increased with each condition. The granules were funneled into a tube and received by a cone shaped cup protruding 2.4 cm into the chamber. This feeder which had an inside diameter of 2.2 cm and a depth of 1.8 cm, was attached 7.2 cm above the floor of the test chamber. Water was available from a spout which extend 1 1 cm into the box at a height of 12 cm. During pellet delivery, the spout was placed directly above the feeder tray. For granule sessions however, this spout was moved 4 cm to the left of the feeder hole. The testing room was illuminated by red ambient light emitted from 40 watt light bulbs suspended 10-12 cm above the apparatus. An electric fan provided background noise at 65 db SPL.

Procedure

All subjects were food deprived to 80% of their free- feeding weight prior to testing. Body weight was monitored and maintained at goal levels with daily rations of Purina rat chow. After one week of handling and habituation, a 48 day testing regimen began in which food was available on an FT 60-s schedule for 50 min each day. In Sessions 1-14, the subjects were given pellets in the test chamber as reinforcement for polydipsia training. Once completed, each subject received four granule meals of 0, 14, 21 and 28 s in duration, in random order. Over Sessions 15-46, these treatment conditions were run for 5 days each with 3-day pellet baselines in between. Sessions 44-46 represented the final baseline session after the fourth meal condition. Food powder (0.0-0.2 mm particle diameter) was then manually presented to the animals in the pellet feeder tray for 2 sessions (Sessions 47 & 48). All meals, regardless of texture or duration, were of equal quantity (45 mg +/- 0.5, mean +/- SE). Testing occurred between 0830 and 1630, 5-7 days a week. The final day of each pellet baseline and each granule meal condition was videotaped, as well as the first day of the powder session.

Measures

The volume of water drunk by each subject was recorded to the nearest 0.1 ml on all 48 test days. Additional behavioral measures were provided from videotape and were coded on a microcomputer. All sessions were 50 min in duration and coded as four, 5-min trials. Trial 1 constituted the first 5 min of the session with the remaining trials set at intervals of 10 min each. Each key press signified a specific behavior and was recorded along with the time at which it occurred. Twelve mutually exclusive behaviors were measured including food uptake, taking food into mouth; chew, jaw movements with mouth full; bite, biting anything but food or itself; lick, tongue movements directed at anything but food, water or itself; lick drink, lapping up water splashed into the chamber; drink, drinking water from the spout; groom, scratching, biting, washing and/or licking itself; forepaw action, rapid back and forth movements of the forelimbs (mostly directed at the water spout, feeder cup and corners of chamber), rear, raising forelimbs above feeder cup level; locomote, moving forequarters into one of the four quadrants of the test chamber; immobile, sitting or lying with no movement of any body part; investigate, any movement not involved in the other behavioral categories including mostly sniffing of the chamber area. These behavioral codes and the procedure used to record tham was assessed for both interjudge and test- retest reliability. A greater than 80% agreement was found across all categories and all measures from selected sessions.

Data analysis included not only volume measurements but quantification of each coded behavior. For this study, a bout can be said to represent one occurrence of a behavior. The percentage of total trial time (percent time, PT) spent engaged in a behavior was calculated for statistical investigation. In addition, bout frequency (BF) represented how often a behavior occurred within each trial and session. Finally, the mean bout duration (BD) of each behavior was analyzed after normalizing the data with the transformation square root (1 plus BD score in seconds). ANOVA with repeated measures conditions, sessions or trials were obtained for each of the aforementioned behavioral measures where appropriate. The Geisser Greenhouse correction factor ($\epsilon = 1/t-1$) was applied in order to account for heterogeneity of covariance. Every significant F ratio was subjected to either Newman-Keuls or Tukey's HSD (when greater than 10 means were being compared) tests for multiple comparisons ($p<.05$).

Results

Upon analysis of water consumption, one way ANOVA across the 14 days of polydipsia training revealed a significant sessional effect, $F(13,169) = 24.43$, $p<.005$ (data not shown). In Sessions 1 and 2, the rats drank significantly less water than in Sessions 4 through 14 (Tukey's HSD). After Session 5, no further increases in water volume levels were revealed suggesting that polydipsia was established and maintained after this point. Pellet Session 14 was used as a comparison session for subsequent treatment sessions. ANOVA across all six food conditions was significant in that powder water volumes were lower than pellet, meal 0, 14, 21 and 28, $F(5,65) = 7.74$, $p<.025$ (Figure III-1). When volumes were considered over sessions within the respective treatments compared to Session 14 of pellet delivery, as shown in Figure III-1, the only significant F ratio was for powder, $F(5,65) = 44.13$, $p<.001$. The two days of powder food delivery had lower water consumption levels than pellet Session 14. By contrast, the coarser granules of varying meal lengths failed to significantly change water intake volumes from polydipsic levels induced with pellet food.

Behavioral analysis involved an examination of each oral activity and its respective relationship with drinking levels. Of the seven oral behaviors coded, only food uptake and drink were found to have significant F ratios after one- way ANOVA across conditions (data not presented for chew, bite, groom, lick & lick drink). PT for food uptake was significant, $F(5,65) = 272.75$, $p<.001$, as well as BF, $F(5,65) = 6.28$, $p<.05$, and BD, $F(5,65) = 294.93$, $p<.001$. Basically, all pellet sessions coded had lower PT scores than all other conditions (Figure III-2). Upon further examination, the data also showed a progressive increase in time spent per session engaged in food uptake with increasing meal length. In other words, meal 0 had lower PT scores than 14 which was in turn lower than 21, etc. In addition, PT for powder was found to be less than meal 28. This information suggests that the finer food texture delivered immediately (0 s) required less time to consume than the 28 s meal of coarse granules. Bout frequencies for food uptake were higher in the 0, 28 and powder conditions compared to pellet (Figure III-2). With respect to BD, Figure III-2 shows the same trend seen with PT scores such that pellet durations were shorter than all other conditions. In addition, meal 0 had shorter bout durations of food uptake compared to meals 14, 21, 28 and powder. Condition 14 also had lower BD scores than the meals of longer duration. Finally, food uptake bout durations were longer during meal 28 than for powder. These BD findings were therefore significantly responsible for the trends found in the PT data for food uptake.

With respect to the behavioral category drink, only the PT measure was significant across conditions, $F(5,65) = 8.47$, $p<.025$. In essence, the amount of time devoted to drinking was lowest in powder sessions compared to all other food conditions (Figure III-2). This finding parallels the data on water consumption since powder had the lowest volumes across food types. When drink was directly compared to food uptake, a small and nonsignificant negative correlation was found across food conditions ($r = -.19$). Virtually no correlation was reported when food uptake was compared to drinking volumes across conditions ($r = .06$). In summary, although food uptake was significantly greater witn each granule meal (including powder), compared to pellet, drinking did not significantly decrease across food types except in the powder session. Therefore, as expected, no inverse correlation between feeding and drinking was found.

Within each condition, a one-way ANOVA was conducted for each oral behavior in order to document any changes across trials (Table III-1, PT scores only). Similarly, any significant effects were examined for inverse relationships between feeding and drinking in any given segment of each session. Food uptake PT scores were significant for three of the food conditions. First, pellet Session 14 revealed Trial 1 was greater than Trials 2, 3 and 4; a finding which held true for both PT and BF scores respectively, $\underline{F}(3,39) = 4.82$, $\underline{p}<.05$ (Table III-1); $\underline{F}(3,39) = 7.37$, $\underline{p}<.025$ (data not shown). The opposite trend was found for PT food uptake in the remaining two conditions, 0 and 21, since Trial 1 was less than Trials 2, 3 and 4 ($\underline{F}(3,39) = 5.54$, $\underline{p}<.05$; $\underline{F}(3,39) = 8.32$, $\underline{p}<.025$). With a two-way ANOVA for these PT data, however, no significant Condition x Trials interaction was found to uphold these opposing trends. Conditions 0, 14, 21 and 28 all had higher Trial 1 PT scores compared to Trials 2, 3 and 4 for the category drink, $\underline{F}(3,39) = 8.17$, $\underline{p}<.025$; $\underline{F}(3,39) = 6.75$,

$p<.025$; $F(3,39) = 11.84$, $p<.005$; $F(3,39) = 5.82$, $p<.05$, respectively. This trend was also true for drink BF in condition 0, $F(3,39) = 5.51$, $p<.05$ (data not shown). Bout durations of drinking were shortest in Trial 4 compared to the beginning of the 0 and 21 sessions, $F(3,39) = 6.65$, 6.49, $p<.025$, respectively. These data suggest that Trial 1 food uptake and drink activity levels are opposite with respect to behavior levels in the remainder of the trials in conditions 0 and 21. Further analysis however, failed to reveal a significant negative correlation for Trial 1 of these oral behaviors.

With respect to the remaining oral behaviors, only bite and groom had any effect across trials (Table III-1). Biting occurred less often in Trials 1 and 2 compared to Trials 3 and 4 but only for the powder PT data, $F(3,39) = 6.32$, $p<.05$. This same trend was seen for grooming during the powder condition, $F(3,39) = 4.35$, $p<.05$. PT groom also showed a significant effect for condition 0 whereby Trials 1 and 2 were greater than the remaining trials, $F(3,39) = 7.79$, $p<.025$. This pattern is opposite in direction to the grooming seen with powder food but is not supported by a significant Condition x Trials interaction after two-way ANOVA. In sum, the oral data showed that rats given pellet food had higher PT scores in Trial 1 for food uptake compared to Trials 2, 3 and 4. For the granule conditions, however, Trial 1 had less time devoted to taking food into the mouth and more time for drinking than in the remainder of the session. Finally, powder food had higher scores for PT groom and bite in Trials 2, 3 and 4 compared to Trial 1.

General activity behaviors were also analyzed across conditions and trials (separate one-way ANOVA's). As illustrated in Figure III-3, PT investigate, locomote and rear all had significant effects across the six food conditions, $F(5,65) = 17.38$, $p<.005$; $F(5,65) = 15.18$, $p<.005$; $F(5,65) = 9.89$, $p<.01$, respectively. For all three behaviors, the pellet condition had higher PT scores than all other food manipulations (excluding powder for the behavior rear). Forepaw action did not show a significant condition F ratio and immobile was not analyzed since this behavior occurred less than 1% of the time. ANOVA across trials for each condition was uninformative except for locomote PT which revealed Trial 1 dominance over remaining trials for both pellet, $F(3,39) = 5.80$, $p<.05$, and condition 0, $F(3,39) = 5.18$, $p<.05$ (data not shown). Basically, in this experiment, the subjects engaged in more general activity behaviors when pellet food was delivered compared to granulated food conditions. For these pellet sessions, more locomoting occurred in the early portion of the session compared to later.

Discussion

After 14 sessions of pellet food delivery on an FT 60-s schedule, it can be established that the subjects were drinking at polydipsic levels. The volume of water at asymptote was over four times higher than in the initial sessions and amounted to greater than 10 ml per g of food eaten. By these measures, compared to the literature (Falk, 1971; Flory, 1971), not only were these rats polydipsic with pellet food delivery, but during granule meal conditions 0, 14, 21 and 28 as well. By contrast, when rats received powder reinforcement, drinking was reduced to half the asymptotic volumes. Although this is a significant decrease in water consumption, it should be noted that this is still twice the amount recorded in the initial sessions. In addition, previous work on powder food and SIP reported water volumes at normal (i.e., pre-polydipsic) levels (Beck et al., 1989, Mumby & Beck, 1988).

The ethological analysis of behavioral activity also revealed specific differences across food conditions. Overall, rat subjects spent more time investigating, locomoting and rearing during pellet food delivery compared to each granule meal condition. This relationship was also true for pellets compared to powder, except for rear where no significant difference was found. In relation to oral activity, one can conclude that pellet sessions required little food uptake time but showed high levels of drinking and general activity. Alternatively, all four durations of granule food required increasing amounts of food uptake time and similarly large amounts of drinking leaving little time for investigate, locomote and rear. Finally, powder sessions with PT for food uptake almost as high as granule meal 28 had less drinking time than all other conditions but levels of general activity within the same range as granule food. Therefore, for all conditions except pellet, it appears that general activity behaviors are a rare occurrence regardless of food particle size.

In considering the aforementioned behavioral analyses, as well as other experimental variables, there are several factors that cannot account for the differences in drinking volumes with food texture. First, the possibility of test chamber differences during the delivery of pellet versus granular food was avoided. Although the motor driving the trickler was not operational during pellet sessions, background noise was provided in an attempt to mask these mechanical differences. For powder food delivery, the pellet dispenser was used to time the food interval even though food was delivered manually. Therefore, reduced drinking in the powder condition was not a function of test environment. Second, satiation could not have led to lower water consumption in the powder condition since the same amount of food was delivered regardless of texture. In addition, granulated food and powdered food were of the same origin and did not differ nutritionally from pellets. Third, the ethological analysis did not reveal that the powder group was engaging excessively in another behavior instead of drink - general activity levels were not higher than for granule foods and no differences were found among the other oral behaviors. Fourth, the interval between each food delivery was fixed at 60 s regardless of condition therefore this is not a factor in producing the observed changes in drinking. It should be considered, however, that since powder food took between 21 and 28 s to consume, the interfood interval could be perceived as less than 40 s in duration. Since SIP has been maintained on schedules as short as 15 s with pellet food (Poling et al., 1980), it is unlikely that any reduction in the schedule parameters can account for the decrease in drinking with powder food. The final and most important factor to be discounted is food uptake time itself. Since varying the meal duration with granulated food did not serve to influence drinking, it is unlikely that the decrease in volume reported for powder is caused in some way by the fact that food uptake took as long as for meal 21 but less than meal 28.

In light of this evidence against alternative factors, it seems reasonable to conclude that meal length is not an important variable in maintaining SIP. Food texture, on the other hand, is the only difference among the food conditions that can sufficiently explain the finding of reduced drinking in powder compared to granules and pellet. As mentioned previously, coarse granules have been shown to induce SIP whereas finer granulations (<0.8 mm) not only prevented acquisition (Mumby & Beck, 1988), but also abolished it once established (Beck et al., 1989). The importance of food consistency has also been documented in that liquid diets fail to produce polydipsi unless they contain sufficient amounts of salt to account for the effect (Poling et al., 1980). It would seem, therefore, that the form in which food is presented is a critical variable in SIP such that coarse food is a minimum requirement.

The conclusions drawn from this study are difficult to explain from a theoretical standpoint. The data do not completely fit the frustration theory approach since drinking is expected to be energized across all food treatments, regardless of texture (Thomka & Rosellini, 1975). Clearly, this was not the case here. Since all meals were of the same mass and moisture content, a dry- mouth explanation (Stein, 1964) also fails to predict the decrease in water intake found for powdered food. Adventitious learning has been criticized because of its inability to state why drinking is the superstitiously reinforced activity, and not some other behavior that occurred in the early sessions (Staddon, 1977). In this study, drinking was polydipsic for many sessions and was decreased when food texture was manipulated - this would not be expected if drinking is considered contiguous with food delivery.

With respect to the theory this study was designed to investigate, the data do not adequately fit with the predictions of the oral substitution hypothesis. An inverse relationship between feeding and drinking levels was not reported across <u>all</u> food conditions. Pellet food has short uptake times and polydipsic levels of fluid intake. Powder food shows the opposite reciprocal relationship (less drinking, more feeding). For the granule meals, however, increasing food uptake times were found from 0 to 28 with no corresponding decrement in the amount of water consumed. Considering that these food uptake time scores were due only to bout duration increases and not bout frequency, one may conclude that bout durations of feeding behavior are not indicative of drinking volumes. In fact, in comparison to the previous experiment where both BF and BD food uptake show significant increases with pit and shell, it could be concluded that the resultant decrease in drinking is due to the BF effect alone. Close examination of the drinking differences between pit and shell also suggested that an increase in the frequency of food uptake in the shell condition could explain its lower volume compared to pit. Therefore, the oral substitution hypothesis and its inverse relationship between feeding and water intake may not be a function of the duration of food uptake, but rather how often this behavior occurs. This may be seen as an explanation for maintenance of the polydipsic response regardless of increased meal duration.

The results of this study can also be accounted for by Wetherington and Riley's (1986) sensitization theory. Sensitization is a form of nonassociative learning characterized by a gradual increase in a response following repeated presentation of a stimulus (Thompson & Spencer, 1966, in Thompson & Donegan, 1986). In the case of SIP, food is considered the eliciting stimulus which, after many repeated presentations, sensitizes water intake such that it shows a progressive increase over sessions. This type of sensitization can be compared to that seen with chronic intermittent injections of amphetamine (Martin-Iverson, in press; Robinson & Becker, 1986). The drug acts as the repeated stimulus which is followed by a gradual enhancement of behaviors such as locomotion and stereotypy, depending on the dose. These behaviors are thus sensitized and are still present weeks or months after drug treatment ceases. The decay time of SIP is still a matter of debate, but some have reported excessive drinking months later (Wetherington & Riley, 1986). In this study, the animals can be said to be sensitized with the pellet food. Switching to coarse granules, which also produce SIP, does not change the drinking response. Powder food, on the other hand, may reduce SIP because the texture of the food is sufficiently different from pellet food so as to effectively remove the eliciting stimulus. Once the eliciting stimulus is no longer presented, the sensitized response no longer occurs - a required feature of sensitization theory. The finding that powder significantly reduced polydipsia but did not abolish it completely in this study could be a function of the strength of the elicting stimulus. Whereas coarse granules may resemble pellets closely enough to sustain the power of food as an elicitor of the SIP response, powder differs just enough to reduce this influence. Afterall, the literature is unsure what effect a reduction in stimulus quality may have on the strength of the sensitized SIP response. In addition, research on feeding behavior and its relation to food size (Whishaw & Tomie, 1989) suggests that rats are sensitive to the form in which food is presented, and how long it will take to consume, and change their behavior accordingly.

In summary, the results of this experiment suggest that food texture, not feeding time, is more important in establishing and maintaining SIP. Powder food reduced drinking volumes whereas granule food did not, despite equal amounts of oral activity with respect to feeding duration. Alternatively, the bout frequency of food uptake may be said to be a better predictor of drinking volumes as suggested by the data in both this study and in the previous pit and shell experiment.

Essentially, when drinking is sensitized by pellet food, the level of water intake can be considerably reduced by increasing the frequency of feeding activity. This relationship is exemplified in the powder, pit and shell conditions where low volumes were associated with high BF food uptake scores compared to pellet sessions. The granule meal conditions, by contrast, showed increasing BD scores for eating which only served to confirm that the experimental conditions were effective in increasing oral activity. No reduction in drinking was found and the frequency of food uptake was not, for the most part, different from pellet. The importance of increased frequency over duration lies in the suggestion that an animal engaging in many separate bouts of a behavior is more aroused or excited than one who performs a behavior for an extended period of time. In other words, these data suggest that arousal or excitation of feeding behavior may block the sensitized drinking response in the SIP paradigm.

The present investigation has raised some interesting questions about SIP and can certainly be improved upon with future research. It would be beneficial to obtain an analysis of activity within the 60-s interfood interval in order to determine when drinking occurred in relation to food delivery. Licking rates could also be examined for possible differences with food texture. Oral movements, particularly tongue protrusions, may be found to differ with food texture. Powder food may involve some mouth activity that competes with, or effectively substitutes for, the act of drinking. In addition, the question of frequency versus duration of eating bouts needs to be further addressed in order to qualify the oral substitution hypothesis. Each of these investigations would help shed light on the finding of food texture being a more salient factor in producing and maintaining SIP than temporal food manipulations.

Table III-1

Mean PT Scores Across Trials for Different Oral Behaviors

Behavior	Condition	Trials 1	2	3	4
Food Uptake	Pellet	1.82	1.51*	1.21*	1.22*
	0	19.96	24.13*	24.62*	27.28*
	14	36.56	37.25	39.12	39.10
	21	42.15	45.88*	46.95*	48.41*
	28	49.05	52.25	52.57	54.58
	Powder	50.79	47.21	43.73	41.85
Drink	Pellet	16.77	18.14	16.04	18.68
	0	25.93	22.01*	20.57*	17.87*
	14	22.75	16.65*	17.21*	14.14*
	21	22.73	19.89*	16.28*	13.54*
	28	21.06	15.38*	13.52*	13.47*
	Powder	5.55	6.40	6.57	7.20
Bite	Pellet	3.24	6.62	6.26	5.11
	0	6.38	8.40	8.88	7.85
	14	5.93	6.84	6.93	6.91
	21	3.40	3.75	4.68	4.81
	28	2.00	3.44	3.49	5.57
	Powder	1.29	3.38	5.31*	4.97*
Groom	Pellet	3.83	4.63	4.81	4.11
	0	4.17	3.54	1.26*	2.02*
	14	3.43	1.93	2.61	2.55
	21	2.67	2.29	2.74	1.29
	28	2.94	1.99	4.46	1.04
	Powder	3.04	3.47	5.82*	5.86*

Note: *SE*'s are less than 20% of significant group means (except for bite and groom).

* $p < .05$ significant difference from Trial 1

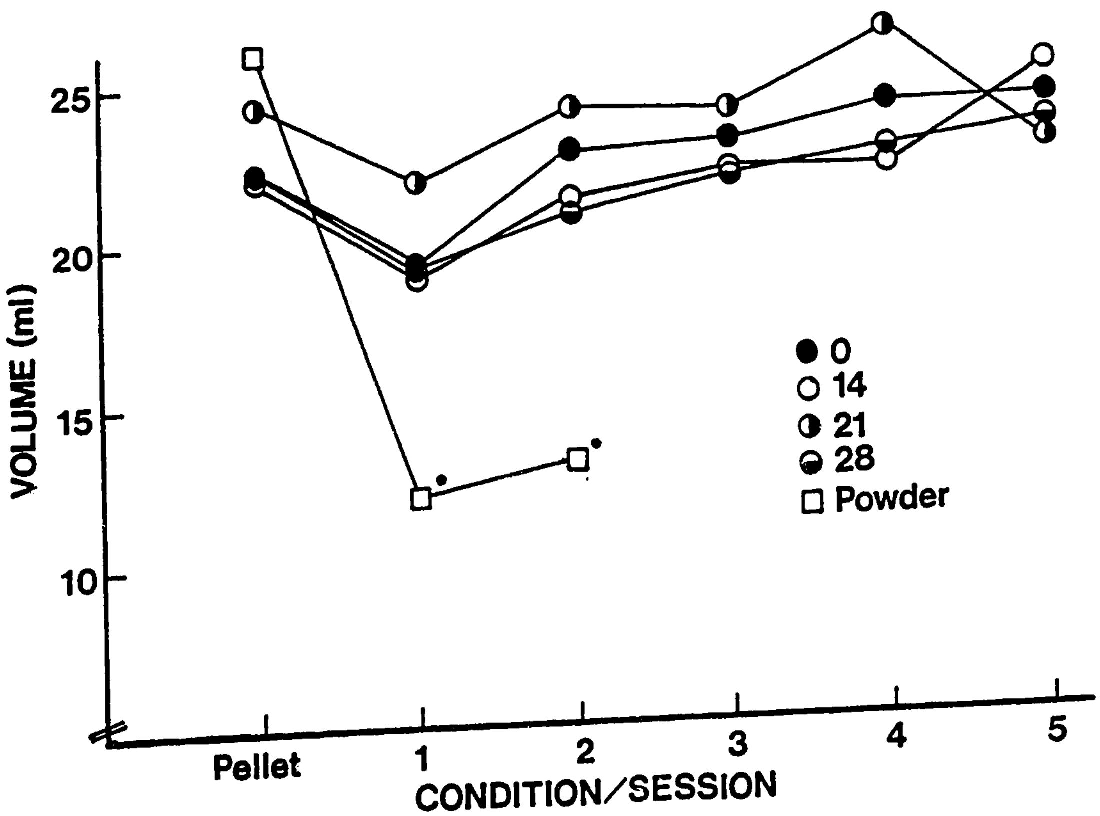

Figure III-1: Volume of water consumed during the pellet condition and each session of the granule meal conditions 0, 14, 21, 28 and powder. Dots denote significant difference from pellet, $p<.05$. SE's are less than 15% of group means.

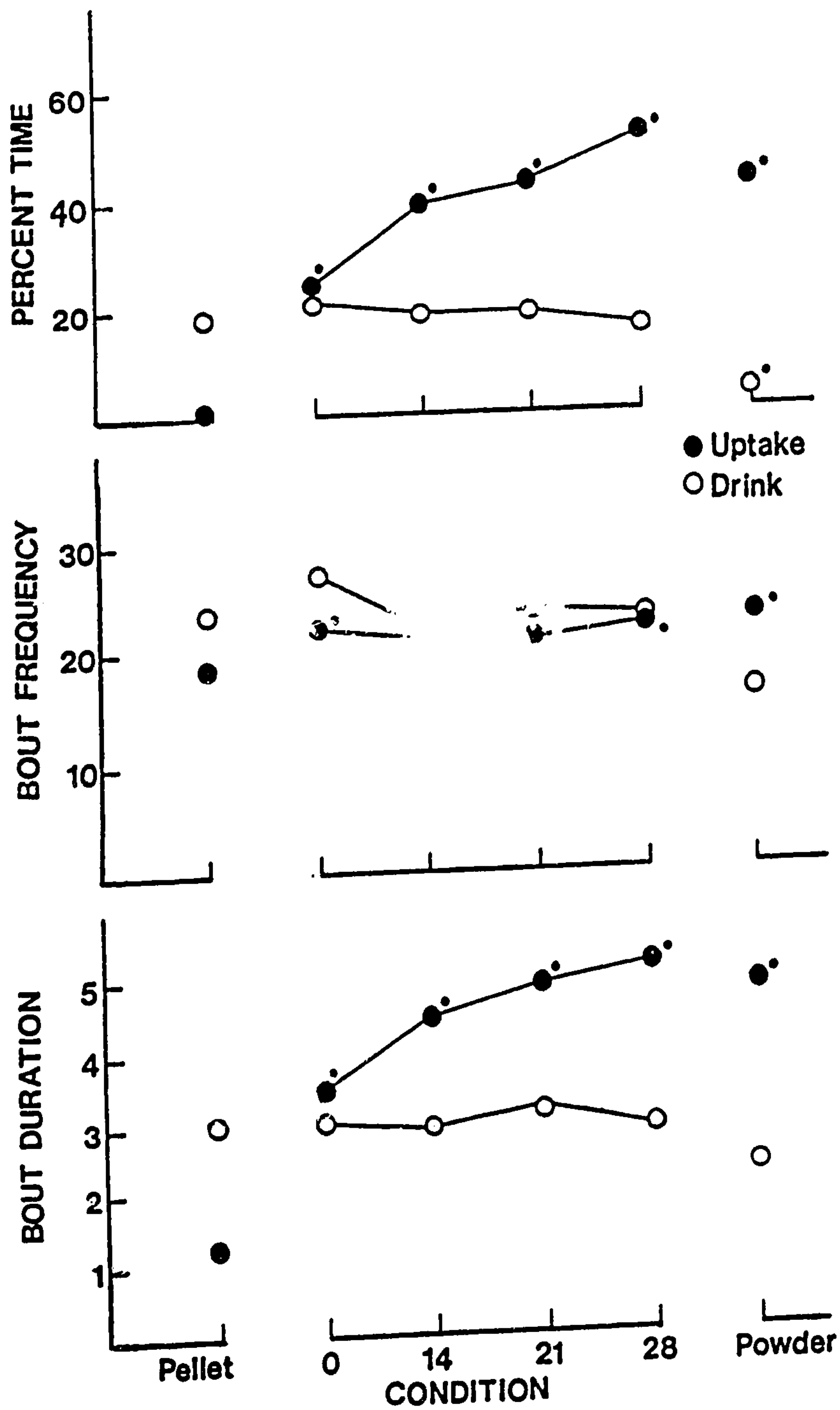

Figure III-2: PT, BF and BD for food uptake and drink in each treatment condition: pellet, 0, 14, 21, 28 and powder meals. Dots denote significant difference from pellet, $p<.05$. SE's are less than 15% of groups means.

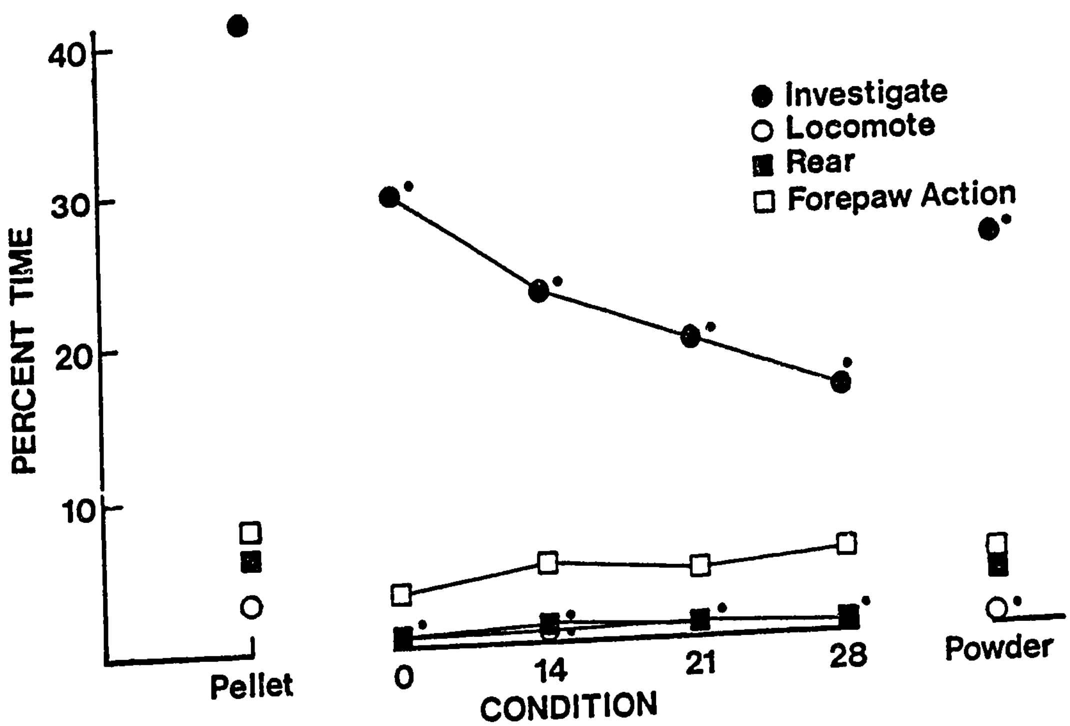

Figure III-3: PT for investigate, locomote, rear and forepaw action across all meal conditions pellet, 0, 14, 21, 28 and powder. Dots denote significant difference from pellet, $p<.05$. SE's are less than 25% of group means.

References

Beck, C.H.M., Huh, T.J.S., Mumby, D.G. & Fundytus, M.E. (1989). Schedule-induced behavior in rats: Pellets versus powder. Animal Learning & Behavior, 17(1), 49-62.

Falk, J.L. (1967). Control of schedule-induced polydipsia: Type, size, and spacing of meals. Journal of Experimental Analysis of Behavior, 10, 199-206.

Falk, J.L. (1971). The nature and determinants of adjunctive behavior. Physiology and Behavior, 6, 577-588.

Flory, R.K. (1971). The control of schedule-induced polydipsia: Frequency and magnitude of reinforcement. Learning and Motivation, 2, 215-227.

Martin-Iverson, M.T. (in press). An animal model of stimulant psychoses. In G.B. Baker, A.A. Boulton & M.T. Martin-Iverson (Eds.), Neuromethods: Vol 19. Animal Models in Psychiatry I. New Jersey: Humana Press.

Mumby, D. & Beck, C.H.M. (1988). Schedule-induced polydipsia: Attenuating effects of decreased size of food granulations. Physiology & Behavior, 43, 375-381.

Pisa, M. (1988a). Motor functions of the striatum in the rat: Critical role of the lateral region in tongue and forelimb reaching. Neuroscience, 24, 453-463.

Pisa, M. (1988b). Motor somatotopy in the striatum of the rat: Manipulation, biting and gait. Behavioral Brain Research, 27, 21-35.

Poling, A., Krafft, K., Chapman, L. & Lyon, D. (1980). Polydipsia induced by intermittent delivery of salted liquid foods. Journal of the Experimental Analysis of Behavior, 33, 337-344.

Reid, A.K. & Dale, R.H.I. (1983). Dynamic effects of food magnitude on interim-terminal interaction. Journal of the Experimental Analysis of Behavior, 39, 135-148.

Robinson, T.E. & Becker, J.B. (1986). Enduring changes in brain and behavior produced by chronic amphetamine administration: A review and evaluation of animal models of amphetamine psychosis. Brain Research Reviews, 11, 157-198.

Roper, T.J. (1983). Schedule-induced behavior. In R.L. Mellgren (Ed.), Animal cognition and behavior (pp. 127-164). North-Holland Publishing Company.

Rosellini, R.A. & Burdette, D.R. (1980). Meal size and intermeal interval both regulate schedule-induced water intake in rats. Animal Learning & Behavior, 8, 647-652.

Staddon, J.E.R. (1977). Schedule-induced behavior. In W.K. Honig & J.E.R. Staddon (Eds.), Handbook of Operant Behavior (pp. 125-152). NJ: Prentice-Hall.

Stein, L. (1964). Excessive drinking in the rat: Superstition or thirst? Journal of Comparitive & Physiological Psychology, 58, 237-242.

Thomka, M.L. & Rosellini, R.A. (1975). Frustration and the production of schedule-induced polydipsia. Animal Learning & Behavior, 3, 380-384.

Thompson, R.F. & Donegan, N.H. (1986). The search for the engram. In J.L. Martinez, Jr. & R.P. Kesner (Eds.), Learning and Memory: A Biological View (pp. 3-52). FL: Academic Press, Inc.

Timberlake, W. & Allison, J. (1974). An empirical approach to instrumental performance. Psychological Review, 81, 146-164.

Wetherington, C.L. & Riley, A.L. (1986). Diminution of schedule-induced polydipsia after a long rest period. Physiology & Behavior, 37, 375-378.

Whishaw, I.Q. & Tomie, J. (1989). Food-pellet size modifies the hoarding behavior of foraging rats. Psychobiology, 17, 93-101.

Yoburn, B.C. & Flory, R.K. (1977). Schedule-induced polydipsia and reinforcement magnitude. Physiology & Behavior, 18, 787-791.

IV. General Discussion and Conclusion

The purpose of the studies discussed herein was to specifically test the oral substitution hypothesis of SIP with different food manipulations. An additional focus was to further understand the parameters behind oral substitution in an attempt to discover if the amount of oral activity associated with feeding is a function of time or texture.

In the first study entitled "Attenuation of Schedule-Induced Polydipsia With Increased Feeding Activity: The Oral Substitution Hypothesis", an inverse relationship between feeding and drinking was documented. Essentially, the pit and shell food treatments increased the amount of oral activity associated with feeding and subsequently abolished SIP. This result not only replicates previous research (Beck et al., 1989; Reid & Dale, 1983), but, more importantly, supports the oral substitution hypothesis. In addition, the reported differences between pit and shell with respect to drinking and food uptake suggest that the form in which food is presented may influence oral substitution.

The second experiment, as suggested in its title "Maintenance of SIP With Increasing Granule Meal Durations", failed to support the basic premise of the oral substitution hypothesis. Increasing the amount of feeding behavior with meal length did not reveal a reciprocal decrease in the level of water intake. This finding suggests that temporal factors are not as important to SIP as food texture since coarse granules and pellet food sustained SIP but the powdered food condition diminished it. This result occurred despite the fact that food uptake time was equally long for powder as it was in the longer granule meals. Therefore, as suggested by the previous study, the quality or type of food appears to be a more salient feature in establishing and maintaining SIP than the temporal properties of the meal.

The data presented in these experiments can be approached from the sensitization point of view suggested previously. According to Wetherington and Riley (1986), SIP is a sensitized response to the repeated presentation of an eliciting stimulus (food). Drinking does not immediately reach polydipsic levels because this sensitization process takes time to develop--approximately 5 days in both of these studies. The results may point to pellet and coarse granules as being sufficiently similar as eliciting stimuli, that switching between the two does not diminish the sensitized drinking response. Pit, shell and powder, on the other hand, do not sustain established SIP because they differ markedly from the original food as elicitor (i.e., pellet). This failure to present the appropriate stimulus results in the absence of the sensitized response. Similarly, in those studies in which powdered food was unable to establish a SIP response from the beginning (Beck et al., 1989; Mumby & Beck, 1988), it may be said that the appearance or quality of the eliciting stimulus was insufficient to produce a sensitized response.

The implications of these findings for the oral substitution hypothesis, however, are more difficult to explain. Since a specific food texture previously shown to induce SIP did not result in a decrease in drinking when oral activity associated with consumption was increased, the oral substitution hypothesis can be said to be an insufficient explanation of this phenomenon. However, when the data are examined more closely, it is apparent that the most important difference between the two studies, besides the drinking levels, is the bout frequency of food uptake. More specifically, pit and shell treatments decreased drinking volumes with an increase in both BF and BD measures of food uptake. The granule meals, on the other hand, had progressive increases in BD food uptake, but not BF, and no concomitant reduction of SIP. From this, it may be concluded that BD food uptake is a poor predictor of drinking volumes thereby suggesting the BF measure is the key to the inverse feeding-drinking relationship. More research needs to be done to clarify this issue and further specify the nature of the oral substitution hypothesis.

In order to fully support the sensitization processes described in this thesis, future study is required regarding the effect of food quality on its ability to act as an eliciting stimulus. In addition, experiments that specifically describe the type of oral activity associated with the consumption of different food types will be informative in understanding the notion of oral substitution. It may well be that coarse food has different oral requirements than powder and liquid such that the latter texture demands tongue or jaw movements that either impede or substitute for the oral activity involved in drinking. A consideration of the striatum and its role in SIP would also provide a more complete description of the oral substitution hypothesis. In the meantime, the findings presented here have succeeded in not only replicating previous work regarding the effects of different food texture on established SIP, but have also extended the knowledge base of this phenomenon to eliminate temporal factors in oral substitution.

References

Beck, C.H.M., Huh, T.J.S., Mumby, D.G. & Fundytus, M.E. (1989). Schedule-induced behavior in rats: Pellets versus powder. Animal Learning & Behavior, 17(1), 49-62.

Mumby, D. & Beck, C.H.M. (1988). Schedule-induced polydipsia: Attenuating effects of decreased size of food granulations. Physiology & Behavior, 43, 375-381.

Reid, A.K. & Dale, R.H.I. (1983). Dynamic effects of food magnitude on interim-terminal interaction. Journal of the Experimental Analysis of Behavior, 39, 135-148.

Wetherington, C.L. & Riley, A.L. (1986). Diminution of schedule-induced polydipsia after a long rest period. Physiology & Behavior, 37, 375-378.